

able for growth. That these plants can survive such a prolonged period of adverse moisture conditions is a striking indication of their xerophytic adaptiveness.

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CYTOLOGICAL OBSERVATIONS ON SOME GENERA OF THE AGAVACEAE

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Even before Hutchinson (1934) set up the family Agavaceae to include tribes of woody xerophytes from both the Liliaceae and the Amaryllidaceae, McKelvey and Sax (1933), Whitaker (1934), and Sató (1935) pointed out that *Yucca* and *Agave*, together with certain of their allies, must be related because they all have a basic karyotype of 5 long and 25 short chromosomes. This karyotype is too unusual to have been developed along two different evolutionary lines.

Since the new family has been constituted there have been numerous comparative studies of the genera within the family evaluating the evidence for and against the erection of the family (Moran, 1949; Wunderlich, 1950; Cave, 1953). According to many botanists today there is strong evidence for a close relationship of *Yucca* and *Agave*, but their agreement with Hutchinson to place these genera with others such as *Cordylina*, *Dracaena*, *Sansevieria*, *Phormium*, *Nolina*, *Dasyllirion*, and *Doryanthes* is not so strong.

One of the lines of cytological evidence useful in taxonomy is the study of the karyotype. Granick (1944) has summarized the information of that date concerning the chromosome numbers in the Agavaceae. Both *Yucca* and *Agave* appear to have widespread hybridization within each genus, but polyploidy so far has been reported only in the latter. Granick discussed polyploidy within *Agave* and concluded that the karyotypes were of little value in determination of individual species, but that there was a definite correlation between polyploidy and vegetative development. The polyploids appear also to have a wider distribution than the diploids. Her counts were made on root tip materials which offer little information as to the possible hybrid nature of the plant examined, especially in the polyploids.

The comparatively long time needed for most of the Agavaceae to mature is probably one of the reasons more cytotaxonomic work has not been achieved on the family. Recently a number of specimens growing at the University of California Botanical Garden, Berkeley, have flow-

ered, and thus an opportunity to study their meiotic chromosomes was presented. In line with the cytological program of the Garden, chromosome numbers of these plants, as well as those of three additional species from material fixed in the wild, have been determined. This paper presents information that may be helpful in future cytotaxonomic studies of the family.

In making chromosome counts flower buds were fixed in three parts absolute alcohol to one part glacial acetic acid. Anthers were squashed in aceto-carmin and slides were made permanent according to the technique of Bradley (1948). Immediately following the name of the species is the number of the permanent slide and the next number is the University of California Botanical Garden cultivation number. These are followed by the place of collection, collector, and the herbarium in which vouchers are deposited. The species of *Agave* are arranged by subgenera according to the classification of Berger (1915). *Agave*, *Furcraea*, and *Beschorneria* have a basic karyotype of 5 long (L) and 25 short (s) chromosomes; *Nolina* and *Doryanthes* do not.

AGAVE, SUBGENUS MANFREDA

A. sp. (5805; UCBG 56.624-1; Mexico, origin unknown). $n = 30$. Meiosis in PMC's was regular with $5L + 25s$ chromosome pairs (fig. 1). The plant was growing in the greenhouse, but has now been set outdoors.

A. sp. (62126; near San Luis Potosi, Mexico, *Kimmach 294*). $n = 30$. Buds collected and fixed in the wild gave a count of $5L + 25s$ chromosome pairs in regular meiotic behavior (fig. 2). Identification and herbarium voucher must await flowering of the specimen at present in the Huntington Botanical Garden.

AGAVE, SUBGENUS LITTAEA

A. filifera Salm-Dyck. (6106; UCBG 60.328-1; Mexico, origin unknown; UC). $n = 30$. This is an ordinary diploid with $5L + 25s$ chromosome pairs. No irregularities were noted in meiosis (fig. 3). This number agrees with that of Horowitz (McKelvey and Sax, 1933).

A. lechuguilla Torr. (6266; UCBG 57.475-1; Texas, Helotes, *O. Sokol*; UC). $n = 55-60$. Granick counted the chromosomes in root tips of three specimens of this species and lists $20L + 100s$ in each. In our plant II M in PMC's gave counts of $10L + 45-50s$ (fig. 4). It is possible that in some instances some of the small chromosomes were missed. Meiosis was regular, with only rare lagging of small chromosomes at I A, and numerous capsules were produced along the raceme-like inflorescence. A few mature seeds were formed.

A. victoria-reginae T. Moore. (6274; UCBG 57.494-1; Mexico, origin unknown; UC). $n = 30$. This species has $5L + 25s$ pairs of chromosomes. Meiosis was regular (fig. 5). No seed was set, however.

A. celsii Hook. (62119; UCBG 49.2087-1; Mexico, Huntington Botanical Garden #20.128; UC). $n = 30$. This is also a diploid with $5L + 25s$

pairs of chromosomes. Meiosis was regular (fig. 6). Capsule formation was heavy, but seed set was negligible.

A. toumeyana Trel. (UCBG 62.254-1; Arizona, origin unknown; UC). This species is probably a polyploid, judging from the number of long



FIGS. 1-9. Chromosomes of *Agave* species: 1, *Agave* sp. (*Manfreda*), I T, polar view, $n = 30$; 2, *Agave* sp. (*Manfreda*), I T, side view, $n = 30$; 3, *Agave filifera*, I M, $n = 30$; 4, *A. lechuguilla*, II M, $n = 58$; 5, *A. victoria-reginae*, I M, $n = 30$; 6, *A. celsii*, diak., $n = 30$; 7, *A. deserti*, diak., $n = 59$; 8, *A. salmiana*, diak.; 9, *A. asperima*, microspore mitosis, $n = 87$. All $\times 833$.

arms of chromosomes in II M. However, meiosis was so disturbed that no count was possible. Like other irregular meioses the development of PMC was not synchronous, but all stages of meiosis were found together in one portion of an anther.

AGAVE, SUBGENUS EUAGAVE

A. deserti Engelm. (6289; UCBG 52.1911-1; Baja California, Mexico. *Hutchison* 710; UC) $n = 59$. This specimen had 10L + 49s chromosome pairs (fig. 7). Meiosis was regular with 10 pairs of large chromosomes and only little lagging at I A. No multivalent formation was noted. Many capsules developed to a large size, but only a very few mature black seeds with embryos were present. Seeds without embryos were the same size, but remained white.

A. salmiana Otto. (62103; UCBG 61.1518-1; Mexico, origin unknown; UC, US, MO). This species was reported by Vignoli as quoted by Granick (1944) to be tetraploid. Meiosis in our plant was so disturbed that a count was impossible at this stage. Development of PMC was not synchronous, but each cell was likely to be at a different stage of meiosis. There were only 5 units that could be considered as associations of large chromosomes, but the number of small chromosomes was considerably greater than 25 (fig. 8). Whether these small units represented pairs or univalents was impossible to say. At I A many bridges and fragments or lagging small chromosomes were present. At the tetrad stage micronuclei were seen which persisted even after the young pollen grains were formed. In pollen grain mitoses 8-9 large chromosomes could often be made out, suggesting that the large units at I M were multivalents. The pollen grains varied in size and the exine might be said to be malformed, in that the pore was enormous, sometimes being about a fourth of the surface of the grain. The walls were thick and sculptured and the grains were often held together in pairs. At maturity some showed two male gametes, while others had only one, or even none, judging from the lack of stainability.

A. asperima Jacobi. (5909; UCBG 49.2095-1; Mexico, Huntington Botanical Garden #20.192; UC). $n = 74-93$. This plant had developed beyond the stage of meiosis in PMC before the present investigation was started. However, divisions in many pollen grains were studied. The pollen did not vary greatly in size and few empty grains were observed. The exine, though sculptured, was not as thick as in *A. salmiana*. In 27 grains in which metaphase plates were counted, there were 16 large chromosomes, one of which was slightly smaller than the rest. In 22 of these plates the small chromosomes could be counted, and ranged in number from 58 to 77 (fig. 9). Counts of small chromosomes cannot be as accurate as those of large. The error should cause underestimation of the number, since it is fairly easy to miss some of the small chromosomes. *A. asperima* is therefore a hexaploid with one large chromosome extra. It would seem that the small chromosomes may segregate unevenly

at meiosis without affecting the viability of the pollen to develop at least through the microspore division. Doughty (1936) reported a variable number of small chromosomes within each of the high polyploid species



FIGS. 10-17. Chromosomes of *Agave*, *Furcraea*, *Beschorneria*, *Nolina*, and *Doryanthes*: 10, *Agave vexans*, II T, $n = 87$; 11, *Furcraea andina*, diak., $n = 30$; 12, *Beschorneria yuccoides*, diak., $n = 30$; 13, *Nolina parviflora*, diak., $n = 19$; 14, *N. bigelovii*, diak., $n = 19$; 15, *N. bigelovii*, I M, $n = 19$; 16, *N. beldingii*, diak., $n = 19$; 17, *Doryanthes palmeri*, I M, $n = 24$. All $\times 833$, except 14 and 16 which are $\times 770$.

studied by him. Sharma and Bhattacharyya (1962) report variation in somatic cells of a number of species in the number of small chromosomes present, and suggest that this irregular behavior may be an aid to speciation in the genus, particularly since various types of vegetative reproduction are common. Unfortunately nothing is known as to whether the mature pollen of *A. asperrima* is viable, or what sort of seed set occurred on this plant.

A. vexans Trelease. (62132; UCBG 49.2089-1; Mexico, Huntington Botanical Garden #20.157B; UC, US, HEID). $n = 87$. This species is also a hexaploid. Meiosis was regular with respect to the large chromosomes. Multivalents were rare in both large and small chromosome pairs. At I A occasional lagging small chromosomes could be seen, but tetrads were normal and there were no micronuclei. At II T (fig. 10) there were 15 large chromosomes and 72 small.

It is of interest that even though meiosis is regular and pollen is apparently good in many agaves, seed set may be negligible or entirely lacking under botanical garden conditions, at least, e.g., when there is only one plant of a species in bloom at one time. Widespread vegetative reproduction in the genus may favor the retention of self-incompatibility factors.

FURCRAEA

F. andina Trelease. (62104; UCBG 61.1490-1; South America, origin unknown; UC). $n = 30$. There were 5L + 25s pairs of chromosomes (fig. 11). No irregularities were observed. Pollen grains remained in tetrads. Seed was not set, but bulbils were produced.

BESCHORNERIA

B. yuccoides C. Koch. (6222; UCBG 57.384-S1; Chiapas, Mexico, *MacDougall 377*; UC, US, K). $n = 30$. The 5L + 25s pairs of chromosomes were microscopically indistinguishable from those of *Furcraea andina* (fig. 12). The pollen grains were also held together in tetrads. Seed set was good, but no bulbils were formed as in the latter genus. The count agrees with Koepferich's findings of 1930, although she reported 12L + 48s chromosomes in somatic cells. One of the largest of the short chromosome pairs must have been considered as long chromosomes.

Except in the genus *Agave* no polyploidy has been reported in any of the Agavaceae with the characteristic karyotype of 5L + 25s chromosomes.

NOLINA

N. beldingii Brandege. (5505; Sierra de la Victoria, Baja California, Mexico, *Carter & Ferris 3331*; DS, UC). $n = 19$. The plants were all male and showed 19 pairs of chromosomes at diakinesis (fig. 16).

N. bigelovii (Torr.) Wats. (5504; In-ko-pah Gorge, Imperial County, California; *Pray s.n.*, in 1955); (6283; near Los Angeles Bay, Baja California, Mexico, *Moran 9732*; SD). $n = 19$. Nineteen pairs of similar-

sized chromosomes were present in meiosis of microsporangiata flowers in both collections (figs. 14, 15).

N. parviflora Hemsl. (6297; UCBG 51.1242-1; Mexico, origin unknown; UC). $n = 19$. This male plant has been growing in the Garden since 1951, having been moved from the main campus. At meiosis there were 19 pairs of chromosomes showing no great differences in size (fig. 13).

Previous counts in the genus *Nolina* have varied. McKelvey and Sax (1933) counted about 38 chromosomes in somatic cells of an unnamed species, and Whitaker (1934) showed 36 chromosomes in the root tips of *N. recurvata*. Lewis (1959) counted 20 pairs in *N. parryi*, although Lenz (1950) pictured only 19 pairs in this species. Satô (1942) showed 36 somatic chromosomes in *N. microcarpa*. Gioelli's count of 10 haploid chromosomes in *N. longifolia*, as reported by Granick (1944) is remarkable in deviating distinctly from those reported for the rest of the genus.

DORYANTHES

D. palmeri W. Hill. (62151; UCBG 32.3895-1; Australia, origin unknown; UC). $n = 24$. This plant has been growing in the Garden since 1932, and has been transplanted three times. An inflorescence appeared in the fall of 1962, and by January 1, 1963 the flowers were in the process of meiosis in the PMC. There were 24 pairs of chromosomes segregating regularly at I A. There was no great difference in size among the pairs, except that one was considerably larger than the rest (fig. 17). Satô (1938) depicts 4 large chromosomes in somatic cells. Although delimitation of microspores was "simultaneous" as in *Phormium* (the only other genus of the Agavaceae with this type of delimitation), the mature pollen grains were monosulcate like those in *Yucca* and *Agave*, and distinctly different from the trichotomosulcate grain of the former.

In the genus *Doryanthes* three different somatic numbers have been reported: in *D. excelsa*, Newman (1929) found 44; in *D. palmeri*, Whitaker (1934) counted 36; in both these species and also in *D. guilfoylei*, Satô (1938) counted 48.

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REVIEWS

Flora of Illinois. By GEORGE NEVILLE JONES. 3rd ed. American Midland Naturalist Monograph 7. vi + 401 pp. Notre Dame, Indiana. 1963. \$7.50.

Jones' *Flora of Illinois* will be familiar to most Midwestern botanists, as it has been for a number of years one of the only up-to-date identification manuals of a Midwestern state. Since Deam's *Flora of Indiana* has been out of print for some years (apparently not to be reprinted in the near future) and the floras of Wisconsin and Michigan are still in preparation, there ought to be considerable local demand for the *Flora of Illinois*.

The general format of the book follows that of the second edition (1950), with one major exception. The usual sequence of families, based on the system of Engler and Prantl, has been abandoned in favor of a modification of that of Hutchinson; a conspectus of this new classification is presented toward the back of the book (pp. 369-373). By and large, Jones appears to have followed the arrangement in such Hutchinsonian works as Clapham, Tutin, and Warburg's *Flora of the British Isles*, but he has introduced some innovations of his own. Unfortunately, some of these modifications are highly questionable, at least if any significance at all is to be placed on the linear arrangement of families. Some of the more debatable assignments in the conspectus include: 1. The Violaceae and Cistaceae are placed in the Papaverales, apparently because of their parietal placentation. As far as I can determine, this is the first time that anyone has ever circumscribed the Papaverales in such a manner. 2. The inclusion of the Lauraceae in the same order with the Lythraceae, 60 families away from the Ranales, is baffling. This assignment is not likely to encourage Hutchinson to claim Jones as a disciple! 3. The Callitrichaceae are placed in the Myrtales between the Haloragaceae and Hippuridaceae. These three families do grow in wet places and tend to have reduced flowers, but there is no good evidence that the Callitrichaceae are any closer to the Hippuridaceae than they are to the Euphorbiaceae (where they were misplaced in the Engler system). 4. The Cactaceae are placed between the Passiflorales and Loasales, despite the fact that much biochemical and anatomical evidence demonstrates their affinity to the Centrospermae (Chenopodiales of Jones). 5. The Aristolochiales are placed after the Myrtales rather than the Ranales. 6. Jones unaccountably rejects one of Hutchin-